Herpetologica, 51(3), 1995, 291–300

MOLECULAR AND MORPHOLOGICAL EVOLUTION IN SOUTH PACIFIC SCINCID LIZARDS: MORPHOLOGICAL CONSERVATISM AND PHYLOGENETIC RELATIONSHIPS OF PAPUAN *LIPINIA* (SCINCIDAE)

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Abstract: I present allozyme data for five species of *Lipinia* (Reptilia: Scincidae) from the South Pacific. These data (1) support the resurrection of *Lipinia rouxi* as a distinct species in congruence with data from nontraditional morphological characters presented by Greer and Mys, (2) show a large degree of genetic divergence between species while data for traditional morphological characters show almost no differentiation, and (3) based on parsimony, support the phylogenetic hypothesis (((*noctua, rouxi, pulchra*) *longiceps*) *leptosoma*).

Key words: Allozymes; *Lipinia*; Morphology; New Guinea; Phylogeny; Scincidae

INSULAR biogeography has played a key role in the understanding of evolutionary processes (Darwin, 1859; MacArthur and Wilson, 1967; Wallace, 1858). Endemism in scincid lizards on South Pacific archipelagos appears to be approximately equal to other more vagile taxa such as birds (Adler, 1992; Adler et al., 1995). Several species of skinks, such as *Lipinia noctua* (Lesson 1830) and *Emoia cyanura* (Lesson 1826 1830), have extremely wide distributions on tropical Pacific islands but show very little morphological differences between archipelagos (Brown, 1991; Burt and Burt, 1932; Ineich and Zug, 1991; Zweifel, 1979). This lack of differentiation of isolated populations is surprising, because the reduced vagility of scincid lizards compared to that of birds should act as a greater barrier to gene flow among populations. One possible explanation for this pattern may be that isolated populations of skinks are in fact genetically differentiated, but due to morphological conservatism, these populations cannot be recognized as distinct species (i.e., cryptic species). Alternatively, dispersal abilities of skinks may be greater than previously thought producing sufficiently large gene flow among populations to prevent morphological differentiation between populations.

In this paper, I examine molecular and morphological variation between five species of the lygosomine scincid genus *Lipinia* Gray 1845 from both island and continental regions of the South Pacific to address questions of morphological and molecular evolution in this group. Specifically, I (1) report allozyme data that confirms Greer and Mys' (1987) observation that *L. rouxi* (Hediger 1934) is a distinct species, (2) examine morphological variation in five species of *Lipinia* for four traditional morphological characters used in South Pacific skink taxonomy and compare this variation with molecular variation, and (3) use these allozyme data to reconstruct a partial phylogeny of the genus *Lipinia* based on four species from the Papuan region and one species from the Belau Islands.

The genus *Lipinia* ranges from southeast Asia, through the Indo-Australian region, and throughout the islands of the Pacific and contains approximately 20 species (Greer, 1974). Within this wide distribution, there are two centers of species abundance: the Philippines where eight species occur (Brown and Alcala, 1980) and the New Guinea region where seven species occur (Greer, 1974; Zweifel, 1979). In this study, I examined five species of *Lipinia*. *Lipinia noctua* has the widest range of any species in the genus, occurring from the Papuan region throughout Oceania to the Hawaiian Islands in the north and the Pitcairn Islands to the south (Zweifel, 1979). *Lipinia rouxi*, in contrast, is restricted to the island of New Ireland, approximately 600 km northeast of New Guinea (Greer and Mys, 1987). *Lipinia longiceps* (Boulenger 1895), occurs from Misima Island east of New Guinea, west across the north coast of New Guinea and loops around south of the central mountain ranges near Etna bay, Irian Jaya (Mys, 1988; Zweifel, 1979). *Lipinia pulchra* (Boulenger 1903), has an apparent spotty distribution along the north coast of New Guinea (Mys, 1988; Zweifel, 1979). *Lipinia leptosoma* (Brown and Fehlmann 1958) is restricted to the Belau Islands approximately 1000 km northwest of New Guinea.

Lipinia noctua and *L. rouxi* occur in broad sympatry from sea level to approximately 900 m elevation on the island of New Ireland (Greer and Mys, 1987; personal observation) (Fig. 1). Zweifel (1979) was unable to distinguish any diagnosable scutellation differences between *L. noctua* and *L. rouxi* and thus placed *L. rouxi* in the synonymy of *L. noctua*. Recently, however, Greer and Mys (1987) found several nontraditional morphological characters that distinguish *L. rouxi* from *L. noctua*. Their diagnostic character was mode of reproduction; *L. rouxi* is oviparous while *L. noctua* is ovoviviparous. Additionally, *L. rouxi* has lost the left oviduct and thus lays only one egg, while both oviducts are functional in *L. noctua*. Other characters used by Greer and Mys (1987) to distinguish *L. rouxi* from *L. noctua* include the absence of visceral fat bodies, absence of a light occipital spot, more posterior location and lighter coloration of the mediodorsal stripe, lack of darkened headshield edges and several other coloration differences which pertain to live specimens (Fig. 2). Based on a limited sample of both *L. rouxi* and *L. noctua*, they also found that *L. rouxi* tends to be smaller (in snout–vent length: SVL) and have more subdigital lamellae. After considering all the available morphological data and field observations, they suggested that *L. rouxi* represents a distinct species and should be resurrected.

While on New Ireland from 24–31 October 1991, I collected 20 specimens of *L. rouxi* and 32 specimens of *L. noctua*. This series of *L. rouxi* more than doubles the number of specimens collected to date [type series $n = 8$, Naturhistorisches Museum in Basel (NHMB) 11683-90; $n = 7$ Institut Royal des Sciences Naturelles de Belgique (IRSNB) 27018/reg. 14322]. All 20 specimens of *L. rouxi* were collected near Lengkamen village on the Lelet Plateau, New Ireland (Fig. 1). Lengkamen is located at approximately 900 m elevation, and the habitat consists of primary and secondary growth forest interspersed with garden areas. All *L. rouxi* were collected by hand and were found on large (>1 m diameter) typically vine-covered trees. Two specimens of *L. noctua* were also collected in the same area also on large trees. Thirty specimens of *L. noctua* were collected at

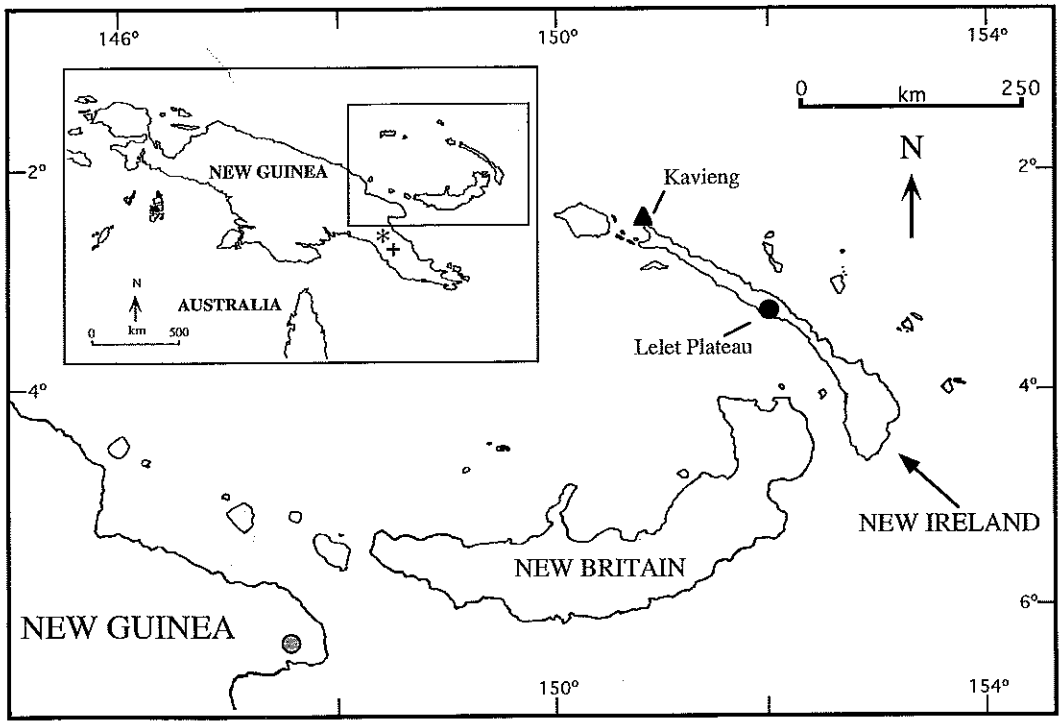

FIG. 1.—Collection localities for *Lipinia rouxi* (solid circle), *Lipinia noctua* (solid triangle), *Lipinia longiceps* (cross), *Lipinia pulchra* (cross), and *Sphenomorphus jobiensis* (cross, asterisk, and stippled circle) from Papua New Guinea. See Appendix I for exact locality information.

sea level near Kavieng, New Ireland (Fig. 1). Morphological but not molecular data were collected from the two specimens of *L. noctua* from the Lelet Plateau.

Although the intra- and intergeneric relationships of many lygosomine skinks remain unresolved, morphological data support the monophyly of the clade of lygosomine scincid genera *Scincella, Ablepharus, Lobulia, Papuascincus, Lipinia,* and *Prasinohaema* (the "Group I" skinks: Allison and Greer, 1986; Greer, 1974). *Sphenomorphus jobiensis* (Meyer 1874) was therefore chosen as the outgroup taxon for the phylogenetic analysis, because this genus certainly represents an outgroup to the Group I skinks and therefore to *Lipinia* (Greer, 1974).

METHODS

Animals

Between August 1991 and January 1992, I collected specimens and tissue samples (muscle and liver) from four species of *Lipinia* from Papua New Guinea. The species were *L. noctua, L. rouxi, L. pulchra,* and *L. longiceps*. Tissue samples from *L. leptosoma* from Belau were made available by Robert Fisher (University of California at Davis). All specimens used in this study are listed in Appendix I.

Allozymes and Analysis

Muscle and liver tissue samples were dissected from freshly sacrificed specimens, and stored in liquid nitrogen in the field, and transferred to a −80 C freezer. Starch-gel electrophoresis of liver and muscle homogenates followed the methods described by Murphy et al. (1990). I scored 14 presumptive loci using the buffer systems listed in Table 1.

I conducted two types of analyses of the allozyme data. The first was a phylogenetic analysis using parsimony. I coded the data using the locus as the character and genotype for that locus as the character state. Transitions between character states

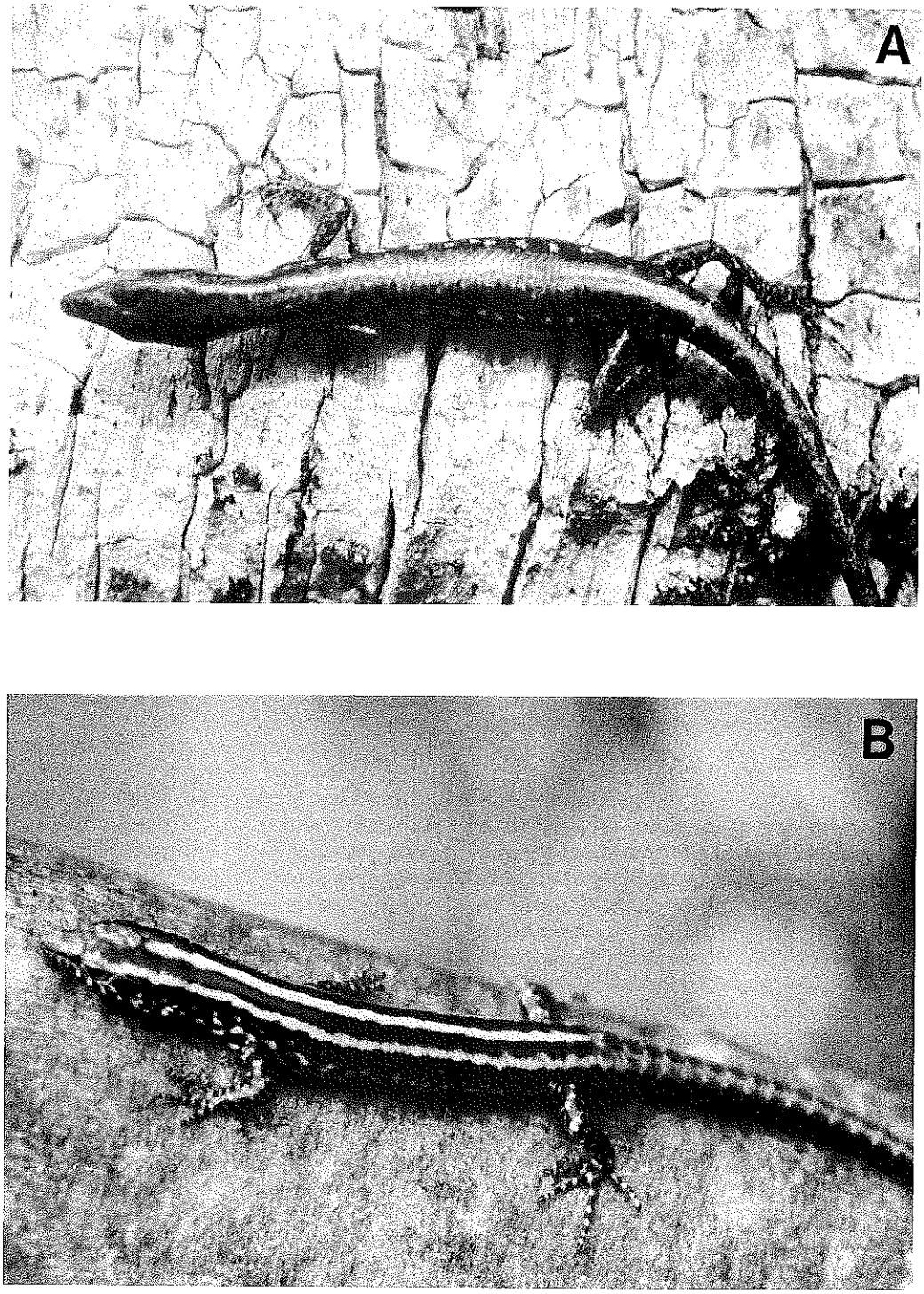

FIG. 2.—(A) *Lipinia rouxi* (TNHC 51432) collected near Lengkamen village on the Lelet Plateau, New Ireland, Papua New Guinea, and (B) *Lipinia noctua* (TNHC 51450) collected near Kavieng, New Ireland. Note absence of occipital spot and more posterior location and lighter coloration of the mediodorsal stripe in *L. rouxi*.

TABLE 1.—The buffer systems, loci scored, and tissue types used in the phylogenetic and distance analyses of the five species of *Lipinia*. Enzymes encoded by more than one locus were designated using Arabic numbers following Shaklee et al. (1989). Buffer type abbreviations are as follows: A = Tris-citrate II (pH 8.0); B = Tris-citrate II (pH 8.0) with 0.02 g NADP added to both gel and buffer; C = Tris-citrate/borate [Poulik] (pH 8.7). Tissue types used were muscle (M) and liver (L). Names, numbers, and abbreviations follow Shaklee et al. (1989).

Enzyme	Enzyme Commission number	Locus	Buffer system	Tissue type
Aspartate aminotransferase	2.6.1.1	AAT	C	M
Aconitate hydratase	4.2.1.3	ACO	B	L
Creatine kinase	2.7.3.2	CK	B	M
Glutathione reductase	1.6.4.2	GR	B	L
L-Iditol dehydrogenase	1.1.1.14	IDDH	C	M
Isocitrate dehydrogenase	1.1.1.42	IDHP	B	L
L-Lactate dehydrogenase	1.1.1.27	LDH-1	B	M
L-Lactate dehydrogenase	1.1.1.27	LDH-2	B	M
Malate dehydrogenase	1.1.1.37	MDH-1	B	L
Malate dehydrogenase	1.1.1.37	MDH-2	B	L
Cytosol aminopeptidase	3.4.–.–	PEP	A	M
Tripeptide aminopeptidase	3.4.–.–	PEPB	C	M
Phosphoglucomutase	5.4.2.2	PGM	B	L
Pyruvate kinase	2.7.1.40	PK	B	M

were weighted using the step matrix protocol of Mabee and Humphries (1993). Origin of a novel allele was considered one step and loss of a preexisting allele also involved one step. An exhaustive search was conducted to guarantee finding the shortest tree, and 1000 bootstrap replicates provided probability values for each node (Felsenstein, 1985).

The second analysis was a phenetic distance method that used genetic distance data to construct a distance Wagner tree. Rogers' and Nei's genetic distances and the distance Wagner tree were computed using BIOSYS-1 (Nei, 1972; Rogers, 1972; Swofford and Selander, 1981).

Morphology

Data for four common morphological characters used in South Pacific scincid taxonomy were summarized from the literature and for the specimens collected for this study. The four characters examined were (1) number of scales around midbody, (2) number of lamellae under the fourth toe of a hind limb, (3) number of paravertebral scales, and (4) maximum SVL. These characters were chosen because they show variation within species and/or populations and thus might be expected to vary between species and are common characters used in taxonomic studies of South Pacific skinks.

RESULTS

Allozymes

Of the 14 loci scored, two (*PEP** and *MDH-1**) were monomorphic for all species. The distributions of alleles in the 12 variable loci are shown in Table 2. The 12 variable loci were subjected to a parsimony analysis using PAUP (Swofford, 1989). Three equally parsimonious trees resulted, each consisting of 52 steps. The strict consensus tree for all three equally parsimonious trees is presented in Fig. 3A. All equally parsimonious trees agree on the monophyly of the *pulchra-rouxi-noctua* clade and depict *L. longiceps* as the sister taxon to the *pulchra-rouxi-noctua* clade, with *L. leptosoma* representing the sister taxon to the *Lipinia* from the Papuan region. The bootstrap analysis was performed to assess confidence in the phylogenetic hypothesis presented in Fig. 3A (Felsenstein, 1985). Bootstrap proportions greater than 50% are reported as circled values in Fig. 3A.

Nei's (1972) and Rogers' (1972) genetic distances are shown in Table 3. The smallest value is a Rogers' distance of 0.286 between *L. pulchra* and *L. rouxi* and the largest is 1.067 between *L. noctua* and *L. longiceps*. The Rogers' and Nei's genetic distances between *L. noctua* and *L. rouxi* are 0.429 and 0.560, respectively (Table

TABLE 2.—Distribution of alleles for the 12 variable loci among the five species of *Lipinia* and the outgroup taxon. Designation of alleles is alphabetic with "*a*" being the most cathodally migrating allele. Allele frequencies are 1 when not shown, otherwise frequencies are in parentheses. Number of individuals sampled (*n*) is indicated in parentheses below each species. See Appendix I and Fig. 1 for localities.

	Lipinia					Outgroup
Protein	*noctua* (*n* = 12)	*rouxi* (*n* = 12)	*pulchra* (*n* = 2)	*longiceps* (*n* = 2)	*leptosoma* (*n* = 3)	*Sphenomorphus jobiensis* (*n* = 11)
*AAT**	*b*	*b*	*a*	*b*	*b*	*a*
*ACO**	*b*	*b*	*b*	*a*	*c*	*b*
*CK**	*b*	*b*	*c*	*a*	*d*	*a*
*GR**	*a*	*c*	*a*	*b*	*e*	*d*
*IDDH**	*a*	*b*	*b*	*b*	*b*	*b*
*IDHP**	*b*	*a*	*a*	*a*	*b*	*b*
*LDH-1**	*a*	*b*	*b*	*b*	*b*	*b*
*LDH-2**	*b*	*a*	*a*	*a*	*c*	*c* (0.91) *d* (0.09)
*MDH-2**	*b*	*b*	*b*	*a*	*a*	*a*
*PEPB**	*c*	*e*	*d*	*c*	*a*	*b*
*PGM**	*a*	*a*	*a*	*a* (0.75) *b* (0.25)	*a*	*a*
*PK**	*b*	*b*	*c*	*a*	*d*	*b*

3). These genetic distances are large when compared to other studies of closely related salamanders (Highton et al., 1989) but are comparable to other lizards (Donnellan and Hutchinson, 1990; Hillis, 1985). Proportions of loci with fixed allelic differences are also shown in Table 3. Six of the 14 loci (43%) examined (*GR**, *IDDH**, *IDHP**, *LDH-1**, *LDH-2**, *PEPB**) show fixed differences between *L. noctua* and *L. rouxi*, indicating reproductive isolation of these two populations (Tables 2 and 3). Additionally, *L. rouxi* shows autapomorphic states for two loci (*GR** and *PEPB**). Rogers' genetic distances were used to calculate a distance Wagner tree using the outgroup method for rooting the tree (Farris, 1972; Swofford and Selander, 1981). The phenogram resulting from the genetic distance data is presented in Fig. 3B.

Both the cladogram and the distance Wagner phenogram place the three taxa *L. pulchra*, *L. rouxi*, and *L. noctua* as a monophyletic clade. The cladogram does not resolve the relationships of these three taxa, while the distance Wagner tree resolves the relationships as *L. pulchra* being the sister taxon to the *rouxi-noctua* clade. The distance Wagner tree differs from the cladogram by grouping *L. longiceps* and *L. leptosoma* as sister taxa as well as providing an estimate of the amount of divergence between species.

To compare the parsimony and distance hypotheses of relationship, I determined the number of additional steps required to fit the data most parsimoniously to the topology resulting from the phenetic analysis. Four additional steps (56 steps total) are required if the topology is constrained to that of the distance Wagner tree. The winning sites test (Prager and Wilson, 1988) for a binomial distribution shows no significant difference ($P = 0.0625$) between the two hypotheses. Two characters are the cause of conflict between the two hypotheses (*IDHP** and *LDH-2**) and both support the parsimony tree.

Morphology

Table 4 presents data for four morphological characters commonly used to distinguish species boundaries in scincid lizards for the five species of *Lipinia* examined in this study. Greer and Mys (1987) stated that *L. rouxi* has more subdigital lamellae and smaller maximum size compared with *L. noctua*. Their statement about maximum SVL remains true for the extended data set but not their statement about lamellae number. Maximum SVL is a poor choice for a character to elucidate size differences between species because

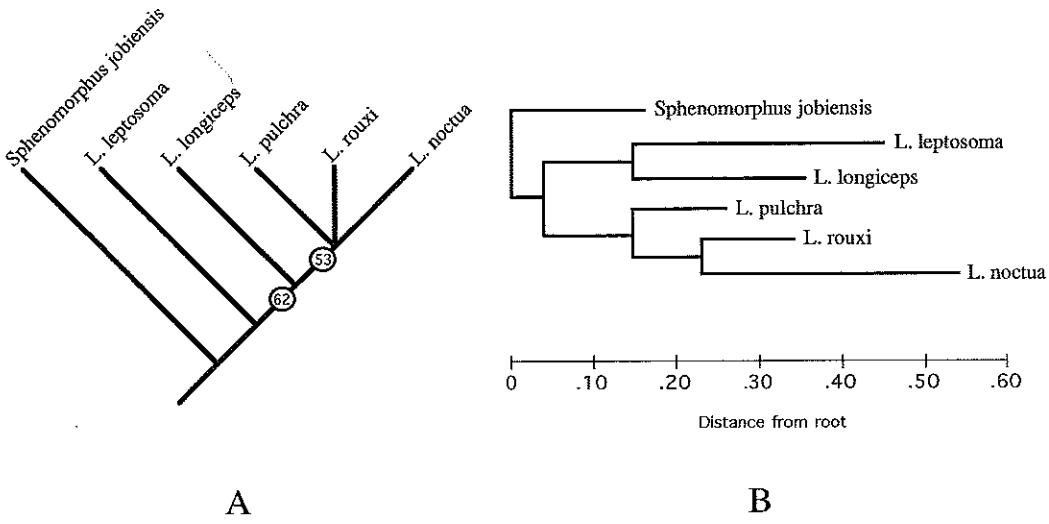

FIG. 3.—(A) Strict consensus tree of the three equally most parsimonious trees. Bootstrap proportions greater than 50% for 1000 pseudosamples are circled. (B) Distance Wagner tree depicting the relationships of five species of *Lipinia* (reconstructed using Rogers' genetic distances and *S. jobiensis* as an outgroup).

of its inferior statistical properties. A more statistically comparable measure of body size between populations or species would be the mean adult female or male body size; if this approach were taken, the differences in body size between *L. noctua* and *L. rouxi* may not be statistically significant. Additionally, the data from the literature for the first three characters are presented as a range without providing values for mean and variance, thus preventing any statistical analysis of these data. Inspection of Table 4, however, clearly illustrates that there is no obvious difference in the character values between species.

DISCUSSION

Scincid lizards have colonized the multitude of oceanic islands in the South Pacific and are the most abundant and visible component of the herpetofauna on these islands. The data presented in this paper demonstrate conservative morphological evolution in the genus *Lipinia* and suggest that a similar pattern may exist in other lygosomine skinks. Recent systematic work on other lygosomine scincid lizards suggests that morphological conservatism may indeed be a general pattern for this subfamily, thereby masking actual species di-

TABLE 3.—Estimates of genetic divergence between five species of *Lipinia* and the outgroup taxon for 14 allozyme loci. Figures above the diagonal are Nei's (top) and Rogers' (bottom) genetic distances (Nei, 1972; Rogers, 1972), and those below the diagonal are proportions of loci with fixed allelic differences.

	1	2	3	4	5	6
(1) *L. noctua*	—	0.560	0.693	1.067	1.030	0.841
		0.429	0.500	0.661	0.643	0.568
(2) *L. rouxi*	0.429	—	0.336	0.578	0.847	0.687
			0.286	0.446	0.571	0.497
(3) *L. pulchra*	0.571	0.357	—	0.716	1.030	0.554
				0.518	0.643	0.426
(4) *L. longiceps*	0.643	0.429	0.500	—	0.716	0.710
					0.518	0.515
(5) *L. leptosoma*	0.571	0.571	0.643	0.500	—	0.674
						0.494
(6) *S. jobiensis*	0.571	0.500	0.500	0.500	0.429	—

TABLE 4.—Comparison of four traditional morphological characters used to distinguish species boundaries in South Pacific scincid lizards for five species of *Lipinia*. Values for *L. noctua* and *L. rouxi* are combined to facilitate comparisons. All values are in millimeters and the first three characters are presented as a range of values. Number of individuals sampled (n) is presented in parentheses below each value.

Species	Number of scales around midbody	Lamellae under the fourth toe	Paravertebral scales	Maximum SVL	Reference
Lipinia noctua	23–27 ($n = 528$)	17–25 ($n = 528$)	47–63 ($n = 528$)	—	Burt and Burt (1932)
	22–28 ($n = 92$)	17–26 ($n = 79$)	44–57 ($n = 76$)	51 ($n = 8$)	Zweifel (1979)
	28–30 ($n = 3$)	17–22 ($n = 10$)	43–51 ($n = 10$)	46 ($n = 10$)	This study
L. noctua combined	22–30 ($n = 623$)	17–26 ($n = 617$)	43–63 ($n = 614$)	51 ($n = 18$)	
Lipinia rouxi	22–28 ($n = 15$)	22–26 ($n = 7$)	47–53 ($n = 7$)	40 ($n = 7$)	Greer and Mys (1987)
	28–30 ($n = 2$)	20–25 ($n = 8$)	43–49 ($n = 8$)	41 ($n = 8$)	This study
L. rouxi combined	22–30 ($n = 17$)	20–26 ($n = 15$)	43–53 ($n = 15$)	41 ($n = 15$)	
Lipinia pulchra	22–25 ($n = 2$)	21 ($n = 2$)	46 ($n = 2$)	40 ($n = 2$)	This study
Lipinia longiceps	24–26 ($n = 2$)	19–20 ($n = 4$)	52–57 ($n = 4$)	40 ($n = 4$)	This study
Lipinia leptosoma	22–26 ($n = 50$)	—	46–54 ($n = 50$)	44 ($n = 30$)	Brown and Fehlmann (1958)

versity (Donnellan and Aplin, 1989; Donnellan and Hutchinson, 1990; Hutchinson et al., 1990). Therefore, either more extensive morphological work, molecular work, or both must be undertaken to realize fully the species boundaries and species relationships of South Pacific scincid lizards. Only once the actual species diversity of skinks is known can one begin to utilize the natural laboratory that is the South Pacific to address questions of comparative biogeography.

Lipinia rouxi does not obviously differ from *L. noctua* for the morphological characters listed in Table 4. Surprisingly, these are common characters used to assess species boundaries in South Pacific scincid lizards (Brown, 1991; Burt and Burt, 1932; Donnellan and Aplin, 1989; Greer and Mys, 1987; Loveridge, 1948; Zweifel, 1979). For example, Burt and Burt (1932) provided a table of the first three characters listed in Table 4 for *L. noctua* from eight Pacific archipelagos showing no obvious differences between archipelagos, and they concluded that these "data indicate that *noctua* has a rather constant range of variation throughout the distributional area concerned" (p. 540). Clearly if *L. rouxi* had been one of the populations surveyed it would not have been recognized as a distinct species. Further, three of the five characters used by Zweifel (1979) in his monograph on variation in *L. noctua* and Papuan *Lipinia* are the first three listed in Table 4.

Lipinia noctua and *L. rouxi* have a large genetic distance (Nei's = 0.560) yet are morphologically very similar. The allozyme data, however, clearly demonstrate that *L. noctua* and *L. rouxi* are distinct evolutionary lineages that show a large degree of genetic divergence. Nontraditional morphological characters also support the specific status of *L. rouxi* (Greer and Mys, 1987). Although species concepts are controversial, *L. rouxi* represents a distinct species based on either a phylogenetic, evolutionary, or biological species concept (Frost and Hillis, 1990). It is thus clear that some of the typical morphological characters used to delineate species boundaries are insufficient in this case. This may be the result of a poor choice of morpholog-

ical characters, reduced morphological evolution compared with molecular evolution, or a combination of both.

The bootstrap analysis suggests that the phylogenetic hypothesis presented in Fig. 3A is moderately supported (Hillis and Bull, 1993; but see Felsenstein, 1993). The *pulchra-rouxi-noctua* clade has a bootstrap proportion of 53 while the *longiceps-pulchra-rouxi-noctua* clade has a bootstrap proportion of 62. These bootstrap proportions are not large but may still reflect real support for these clades (Hillis and Bull, 1993). The phylogenetic hypothesis presented in Fig. 3A places *L. leptosoma*, from Belau, as the sister taxon to the four Papuan *Lipinia*. This suggests that the Papuan *Lipinia* may form a monophyletic clade. The distance Wagner tree (Fig. 3B), however, places *L. leptosoma* and *L. longiceps* as sister taxa which would suggest that the Papuan *Lipinia* do not represent a clade. Clearly additional data are needed to resolve conclusively the relationships of these *Lipinia* and to address the question of whether or not the centers of *Lipinia* abundance in New Guinea and the Philippines represent independent radiations.

Acknowledgments.—I thank the government and people of Papua New Guinea (PNG) whose help made this research possible (PNG export permits 900201, 910230, and 910275 to C. C. Austin). In particular, I thank the people and provincial authorities of New Ireland, Morobe, and Madang Provinces for their help and assistance. I thank M. Kirkpatrick for support (NSF grant BSR-9107140), advice, and encouragement, D. Hillis for providing laboratory facilities, and P. Chippindale for technical advice. Additional thanks go to M. Jebb, L. Orsak, B. Beehler, A. Allison, H. Sakulas, and R. Fisher for advice and help on the field component of this project. Comments by D. Hillis, D. Cannatella, R. Fisher, B. Shaffer, R. Jaeger, and two anonymous reviewers helped improve this manuscript. Specimens of *L. leptosoma* from Belau were collected by R. Fisher. The following institutions provided invaluable funding: Australia and Pacific Science Foundation, Christensen Research Institute (CRI), Explorer's Club, Sigma Xi, National Science Foundation (grant IBN-9311139), Texas Memorial Museum, and The University of Texas at Austin, Department of Zoology. I also thank J. Vindum and J. Gauthier for assistance and use of the California Academy of Sciences' herpetology collection. Field work was conducted at the CRI and the Wau Ecology Institute. This is a CRI contribution publication (CRI Contribution Number 112).

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Accepted: 30 September 1994
Associate Editor: H. Bradley Shaffer

APPENDIX I

Specimens Examined

All specimens, except *L. leptosoma,* were collected by the author and are deposited at the Texas Memorial Museum, Texas Natural History Collection (TNHC). Specimens of *L. leptosoma* were collected by Robert N. Fisher and are deposited at the California Academy of Sciences and may be cross-referenced with their field (RNF) identification numbers.

Allozyme and/or morphological data were collected from the following specimens: *L. rouxi* from Lengkamen village, Lelet Plateau, New Ireland, New Ireland Province (n = 15, TNHC 51421–27, 51431–38); *L. noctua* near Kavieng, New Ireland, New Ireland Province (n = 15, TNHC 51441–47, 51449, 51452–56, 51460–61); *L. noctua* from Lengkamen village, Lelet Plateau, New Ireland, New Ireland Province [n = 2, TNHC 51439–40 (morphological data only)]; *L. pulchra* (n = 3, TNHC 51221, 51283, 51290) and *L. longiceps* (n = 4, TNHC 51222–23, 51284–5) near Bakaia Village No. 1, Garassa, Garaina Valley, Morobe Province; and *L. leptosoma* from the island of Babeldaob, Belau, U.S. Trust Territory of the Pacific Islands (n = 3, RNF 0415, 0419–20). The outgroup taxon used was *Sphenomorphus jobiensis,* collected from three different localities: near Wau, Morobe Province; near Bakaia Village No. 1, Garassa, Garaina Valley, Morobe Province; and near Oligadu, Huon Peninsula, Morobe Province (n = 11, TNHC 51259, 51275–6, 51278–9, 51293, 51317–21).